THE REPRODUCTIVE BIOLOGY OF FEMALE GRIZZLY BEARS IN THE NORTHERN CONTINENTAL DIVIDE ECOSYSTEM WITH SUPPLEMENTAL DATA FROM THE YELLOWSTONE ECOSYSTEM

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Abstract: We analyzed reproductive performance and litter survival for all Northern Continental Divide Ecosystem (NCDE) grizzly bears (*Ursus arctos*) killed or radioinstrumented, 1969-91. Reproductive tracts of 48 female grizzly bears from Montana and Wyoming were described morphologically and examined for corpora lutea and graafian follicles to estimate reproductive potentials for bears in the conterminous United States. The average number of corpus lutea was 2.29. Average cub and yearling litter size was 2.14 and 2.34. Cub survival in the NCDE was 0.887 and yearling survival was 0.863. Sixteen reproductive intervals in the NCDE from 10 individual bears averaged 2.69 years. The minimum age of reproduction in the NCDE varied from 4 to 7 and averaged 5.7 years. Survival of known first litters was not less than survival for litters of experienced females.

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The productivity of female grizzly bears (*Ursus arctos*) and cub survival are important factors in the dynamics of grizzly bear populations. Several studies have provided information on the reproductive biology of grizzly bears (Craighead and Craighead 1969, Hensel et al. 1969, Craighead et al. 1976, Glen et al. 1976). However, detailed studies describing female reproductive biology and productivity in the conterminous United States have been restricted to the Yellowstone Ecosystem. Such data are essential for development of population models and for proper interpretation of population survey and monitoring indexes (Eberhardt 1990). In the Northern Continental Divide Ecosystem (NCDE), numeric recovery targets were established for population productivity (U.S. Dep. of Int. [USDI] 1982). However, little specific data obtained from the NCDE has been assimilated regarding reproductive parameters, productivity, and recruitment for this population.

In this paper, we establish some baseline population biology and productivity parameters which may benefit the establishment of population targets for the NCDE. In addition, we examine the physiological and morphological aspects of reproduction in grizzly bears from the conterminous United States.

We acknowledge K. Greer and the late D. Palmisciano for providing grizzly bear data from reproductive tracts collected at the Montana Department of Fish, Wildlife and Parks, (MDFWP), Wildlife Laboratory, 1969-89. Many field personnel from MDFWP and Blackfeet Indian Reservation (BIR) provided administrative support and field assistance in various portions of the NCDE. Portions of data for this paper come from field projects funded by the Bureau of Indian Affairs, Blackfeet Nation, MDFWP, USDI Bureau of Land Management, USDI Fish and Wildlife Service, and United States Department of Agriculture (USDA) Forest Service.

STUDY AREA

Grizzly bears primarily occur in 2 major ecosystems in the conterminous United States (Fig. 1). The Yellowstone Ecosystem contains grizzly bear habitats within Yellowstone National Park, Grand Teton National Park, and portions of the states of Montana, Wyoming, and Idaho. Grizzly bears are present in more than 5.5 million acres of mountainous terrain surrounded by intermountain valleys and the plateaus and high plains of central Wyoming. The Continental Divide of the Rocky Mountain Cordillera arcs through the southwest quarter of the ecosystem. Elevations range from 1,300 to 3,700 m.

The 5.5 million acre NCDE is mostly rugged mountain topography separated by intermountain valleys. The eastern boundary abuts the high plains and foothills of central Montana. The Continental Divide extends through its middle from Glacier Park south to Rogers Pass. Mountain peaks rarely exceed 3,048 m and valley floors descend to 915 m. The eastern slopes of the NCDE lift in overthrust plates from the 1,372 m high plains.

The climate in both ecosystems is strongly influenced by Pacific maritime air masses from the west and arctic air masses flowing from the north. The oceanic influence decreases from northwest to southeast (Daubenmire 1969).

The vegetation in these ecosystems varies with weather patterns and topography. Most of the habitat includes forested slopes, mountain plateaus, and rocky

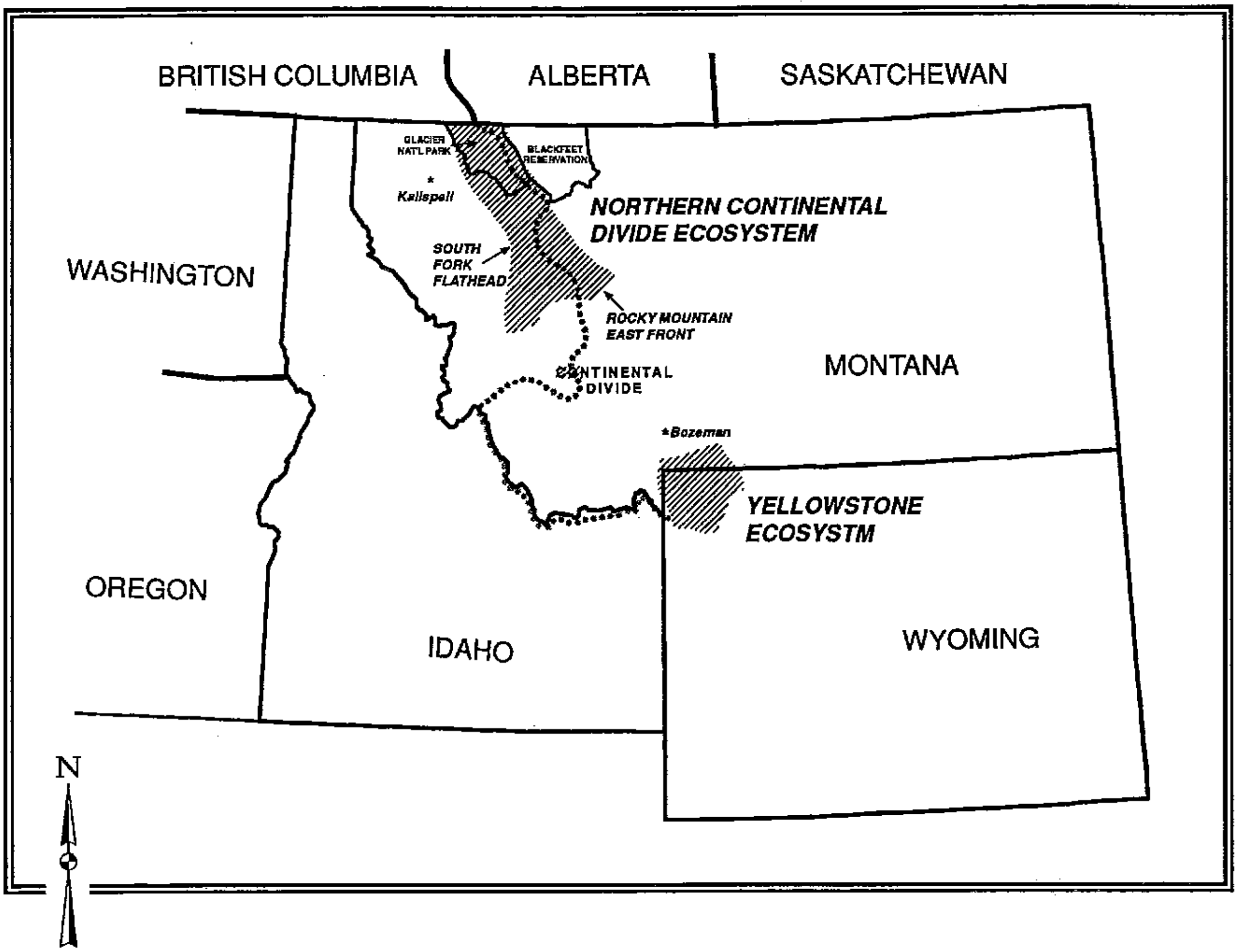

Fig. 1. Map of the Northern Continental Divide and Yellowstone Ecosystems.

peaks with interspersed grassland and meadows. Major forest habitats include limber pine (*Pinus flexilis*), lodgepole pine (*Pinus contorta*), Douglas-fir (*Psuedotsuga menziesii*), whitebark pine (*Pinus albicaulis*), spruce (*Picea* spp.), subalpine fir (*Abies lasiocarpa*), and western red cedar (*Thuja plicata*) (Pfister et al. 1977).

Grizzly bear management programs and United States Fish and Wildlife Service (USFWS) recovery efforts in these ecosystem have been described (Dood et al. 1986, USDI 1982).

METHODS

Gross Examination of Reproductive Tracts

Reproductive tracts were collected from female grizzly bear carcasses resulting from natural or human-caused mortalities, 1969-92. Carcasses examined were from the Yellowstone Ecosystem and NCDE (Fig. 1).

Reproductive tracts were collected during routine necropsies at the MDFWP Wildlife Laboratory in Montana. Tracts were fixed in 10% formalin and stored for later examination. The length of each uterine horn was measured and ovaries were excised. Ovaries were weighed to the nearest 0.1 g and hand sectioned every 2-4 mm to examine macroscopically. The number of corpora lutea and follicular activity were recorded for each ovary pair. Records for each examination were filed in the laboratory necropsy reports for each bear.

We tested for differences in morphological data including carcass weight, placental length, number of corpora lutea, number of graafian follicles, and ovary weights between ecosystems with student's t-tests. Comparisons were also made between subadult bears (<4 years) and adult bears (4+ years). Data were stratified at age 4 because it was the minimum age for reproductive activity.

Age of the bears from which tracts were collected were determined from cementum annuli of multiple roots from premolar teeth (Stoneburg and Jonkel 1966).

Age of First Reproduction and Reproductive Cycles in the NCDE

Age of first reproduction was determined from radio-collared female bears captured during management and research activities, 1979-91. Evidence of first reproduction included observation of cubs and changes in nipple morphology following suckling (Glenn et al. 1976, Aune and Kasworm 1989). Evidence from reproductive tracts such as the presence of corpora lutea and follicular activity provided supportive information to field observations for determining age of first conception and sexual maturity.

Reproductive intervals were determined by monitoring radio-collared female grizzly bears and their litters. A complete interval was defined as the time from birth and den emergence with 1 litter until den emergence with a second and subsequent litter (Craighead et al. 1976). Interval of successful weaning was defined as birth-to-birth intervals without complete litter loss.

Cub Litter Size and Survivorship in the NCDE

Litter size was determined for cub-of-year and yearling litters from radio-collared females on 3 study areas of the NCDE, detailed field reports of family groups in other areas of the NCDE, and from management control actions recorded in the Wildlife Laboratory files, 1969-91. Each cub or yearling litter size was confirmed by multiple radio relocation, live capture of cubs, or examinations of cub carcasses in the case of mortalities. Data on litter size, estrous, and lactation were obtained for each record. Records were stratified by decade (1969-80 and 1981-91), east or west of the Continental Divide, and season. Seasons were defined as spring (April and May), Summer (June-August), and Fall (September-November).

Cub survivorship was determined for radio-collared family groups monitored during research and management efforts from 1978 to 1991. Data were obtained during research efforts conducted on the Flathead drainage, Rocky Mountain East Front and the Blackfeet Indian Reservation, or from management activities in various portions of the NCDE. A complete record for each litter included the female ID number, age, date first detected, cub or yearling litter size, MDFWP region, study location, bear type, and the number of survivors. Percent survivorship of all cub and yearling litters represented the percent of all cubs and yearlings known to survive from field detection, through the denning period and emerge from the den the following year with radio-collared females. Percent survivorship of spring cub and yearling litters represented the percent of cubs and yearlings known to emerge from dens with mothers and survive until emergence as yearlings. The data includes all records of known complete litter loss. Data were stratified by east or west of the Continental Divide, and first litters or litters of experienced mothers.

Ages were determined for each captured and radio-monitored female using cementum annuli counts of extracted premolar teeth (Stoneberg and Jonkel 1966). In several cases previous marking of yearlings and cubs provided known-aged animals.

DATA ANALYSIS

The software package STATGRAPHICS (STSC, Inc 1986) was used for statistical analysis. The student's t and ANOVA tests were used to compare means and age-specific data. A Chi-square test was used to compare categorical data. Statistical significance was 95% unless otherwise stated.

RESULTS

Gross Morphology of Reproductive Tracts

Reproductive tracts from 48 female grizzly bears were examined including 29 from the Yellowstone Ecosystem and 19 from the NCDE. The date of collection ranged from May until October, 1969-92. Thirty-three tracts (69%) were from bears ≥4 years.

There was no difference in mean carcass weight (t = 0.53, P = 0.60) placental length (t = 0.34, P = 0.74) and ovary weight (t = 0.85, P = 0.40) when comparing samples from the Yellowstone Ecosystem and NCDE. Morphological data from reproductive tracts of female grizzly bears in the conterminous United States were pooled to generate a reasonable sample for further analysis.

Mean weight of ovaries from the right and left side of the reproductive tract were not significantly different (t = -0.09, P = 0.92). The weight of ovaries increased until age 4 then stabilized (Fig. 2). The mean ovary weight (1.56 g) of bears <4 years old was

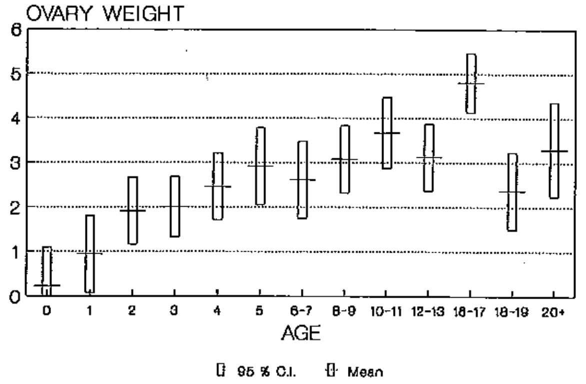

Fig. 2. Mean weight of ovaries by age class for female grizzly bears from the conterminous United States, 1969-91.

significantly less than the mean (3.39 g) for bears ≥4 years (t = 4.71, P = 0.00002). There was no difference in the mean weight of ovaries from bears ≥4 years old when comparing lactating and nonlactating females (t = 0.21, P = 0.83) or females with corpora lutea present in ovaries and those without (t = 0.14, P = 0.89). Regressing the weight of ovaries for bears ≥4 years old against body weight resulted in a significant positive linear regression but the fit was relatively weak (r^2 = 0.28, P = 0.0004) (Fig. 3).

Uterine horn length was measured for 17 females. Mean length of the right (112.2 mm) and left (120.3 mm) uterine horns were not significantly different (t = -0.57, P = 0.57). The mean length of the uterine horns for bears ≥4 years old (146.5 mm) was significantly greater than those <4 years old (82.9 mm) (t = 4.104, P = 0.0009).

Graafian follicles were found in ovaries from 14

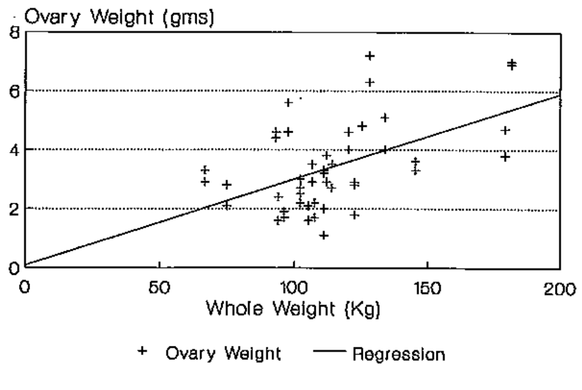

Fig. 3. Ovary weight regressed against whole weight of adult female grizzly bears from the conterminous United States, 1969-91.

individual grizzly bears aged 2-17 years. There was no difference in the mean number of follicles found in ovaries from the NCDE (4.0, N = 5) and Yellowstone Ecosystem (4.5, N = 9) (t = -0.45, P = 0.66). The mean number of graafian follicles found in all ovaries was 4.5 (SD = 3.1) with a range from 1 to 12. Follicles were found in ovaries from 2 adult females with yearlings and from 4 females reported as lactating.

There was no difference in the number of corpora lutea found in ovaries from the Yellowstone Ecosystem and the NCDE (t = -2.79, P = 0.03). Corpora lutea were found in ovaries of 14 female grizzly bears aged 4-19 years. The mean number of corpora lutea in pairs of ovaries was 2.29 (SD = 0.73) and ranged from 1 to 3. Corpora lutea were not found in ovaries from bears <4 years of age. Corpora lutea were found in 3 of 4 (75%) 4-year-old grizzly bears. Corpora lutea were found in 1 lactating female reported with a litter of yearlings.

Minimum Age of Reproduction and Reproductive Cycles in the NCDE

Age of first conception ranged from 3 until 6 years (N = 10). The mean age of first reproduction was 5.7 years and ranged from 4-7 years of age.

Two records of 3-year-old bears breeding in the spring and conceiving to produce a litter at 4 years of age were recorded. One case involved a known-age female from a litter produced by an older radio-marked female.

Four-year-old female grizzly bears commonly conceived. Two of 3 reproductive tracts from 4-year-old bears from the NCDE had corpora lutea. Six 4-year-old female bears were reported in estrous and observed with males during the breeding season. Three (50%) of these produced a cub litter at age 5.

We recorded 16 complete reproductive cycles from 10 individual bears. The mean reproductive interval was 2.69 years and ranged from 2 to 4 years. Seven 2-year intervals were recorded for 2 individual bears during the studies. Mean reproductive interval for cycles resulting in a successful weaning was 2.73 years for all cycles and 3 years when each bear was weighted equally in the average.

Litter Size and Cub Survival in the NCDE

Litter size was determined for 61 (72%) female grizzly bears monitored during research, 16 (19%) mortality records, and 8 (9%) grizzly bears captured during management actions, 1969-91. Cub-of-year litters averaged 2.14 (N = 56) while yearling litters averaged 2.34 (N = 29). There was no relationship between mean cub litter size and female age (ANOVA $F = 1.484$, $P = 0.1632$). Mean cub litter size was not different in the decade 1969-80 (2.00, $N = 24$) compared to 1980-91 (2.22, $N = 32$) ($t = 1.14$, $P = 0.26$). Mean cub litter size was larger east of the continental divide (2.48, $N = 21$) than west of the divide (1.91, $N = 35$) ($t = 3.05$, $P = 0.003$). Mean yearling litter size east of the divide (2.75, $N = 16$) was larger than west of the divide (1.85, $N = 13$) ($t = 4.27$, $P = 0.0002$).

Mean cub litter size was larger for litters first detected in the spring than those not observed until summer or fall (ANOVA $F = 9.24$, $P = 0.0004$) (Fig. 4). In addition there was a higher relative frequency of 3 cub litters in spring than in summer and fall ($\chi^2 = 19.89$, 6 df, $P = 0.0029$) (Fig. 5).

Mean yearling litter size pooled for the summer/fall period (1.89, $N = 9$) was smaller than the mean for spring (2.5, $N = 20$) ($t = -2.49$, $P = 0.019$) (Fig. 5).

Cub survival rate from detection at den emergence until den emergence as yearlings was 0.903 ($N = 62$). The cub survival of all litters regardless of the date of first detection until den emergence was 0.887 ($N = 71$). Cub survivorship east of the Continental Divide was not significantly higher (0.913, $N = 46$) than on the west side (0.840, $N = 25$) ($\chi^2 = 1.61$, $P = 0.20$). Bear cub survival from female bears with their first litters (0.864, $N = 22$) was not significantly lower than the survival of cubs from experienced females (0.898, $N = 49$) ($\chi^2 = 0.32$, $P = 0.57$).

The cause of 1 cub mortality was unknown. Management control of adult females resulted in the death of 3 cubs of the year. Illegal actions resulted in the loss of 1 cub. One suspected incident of male infanticide was reported for 1 cub litter of 3.

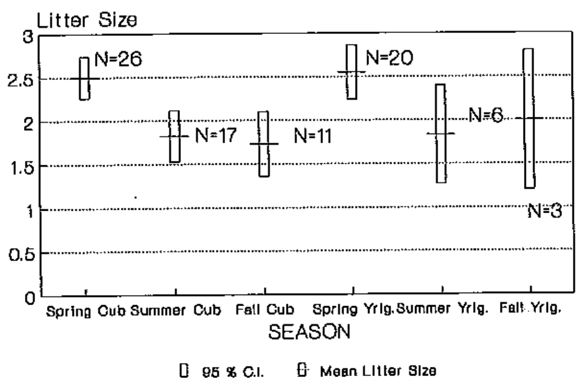

Fig. 4. Mean litter size and 95% confidence intervals for cub and yearling litters by season, 1969-91.

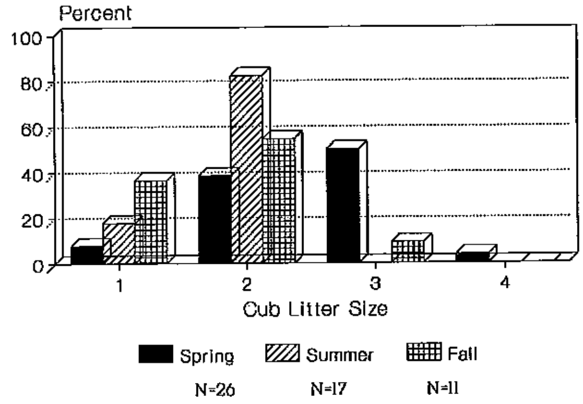

Fig. 5. Distribution of litter sizes for each season for the NCDE, 1969-91.

Yearling survival from spring detection until den emergence as 2-year-olds was 0.86 ($N = 43$). The percent survival of all yearling litters regardless of the date of first detection until emergence as 2-year-olds was 0.863 ($N = 51$). Yearling survivorship was similar both east (0.865, $N = 37$) and west (0.857, $N = 14$) of the Continental Divide ($\chi^2 = 0.06$, $P = 0.94$).

The causes of mortality for yearling bears included management control actions ($N = 3$), natural mortality ($N = 2$), and 1 report of suspected infanticide by a male bear. One yearling died of unknown causes.

DISCUSSION

Gross Morphology of Female Reproductive Tracts

We were unable to collect a large sample of reproductive tracts specifically from the NCDE or the Yellowstone Ecosystem during the past 22 years. The current NCDE female subquota and reduced female mortality within either ecosystem limited opportunities for increased sampling. Statistical tests revealed no difference in variables we examined between ecosystems. Therefore data from reproductive tracts were pooled assuming that basic morphological and reproductive parameters of grizzly bears within relatively close geographic proximity are similar. The pooling of these data allowed us to fully examine reproductive biology of female grizzly bears in the conterminous United States at a time when such information is essential to management.

The mean number of corpora lutea found in grizzly bears from the conterminous United States was slightly higher than the mean number corpora lutea reported for female brown bears in Alaska (Hensel et al. 1969) and type 1 corpora albicantia found in Eurasian brown bear (Tsubota et al. 1990). The survival of embryos and loss of young after birth was unknown. Mean corpora lutea counts were comparatively close to mean litter size reported in field studies. Although there may be significant annual variations in conception rates, embryo abortion, and post-parturition loss, we conclude that the long-term average loss of potential cub production in the NCDE or Yellowstone Ecosystem has probably been relatively low.

Hensel et al. (1969) reported that ovaries of 2-year-old bears were infantile but those from 3-year-olds showed pronounced follicular development. In addition, the authors reported 4-year-olds with placental scars indicating they had bred and conceived at age 3 years and 4 months. Our studies corroborate the findings of Hensel et al. (1969) with the exception that follicular activity might be occurring as early as age 2. Age determinations using cementum annuli counts in our data could be inaccurate and cast some doubt on the results. Additional data from known-age 2-year-old bears would be necessary to confirm the observations of advanced follicular activity.

Reproductive Biology and Cub Survival in the NCDE

In the NCDE some 3-year-old grizzly bears are capable of conception but bears are usually not sexually mature until age 4 years or older. The minimum age of first reproduction in the Montana portion of the NCDE is similar to that reported by Craighead and Craighead (1969) for the Yellowstone Ecosystem and McLellan (1989) for the Flathead region just north of the United States-Canadian border. Pearson (1975) reported the minimum age of reproduction at 6.5 in the Yukon and Miller (1990) reported a mean age at first reproduction of 5.35 years in Alaska. Reynolds (1990) reported age of first reproduction in north-central Alaska at between 5 and 7. Female grizzly bears in the NCDE produce their first litters at a similar or slightly earlier age than grizzly bears from other areas of North America.

Age of first reproduction is likely affected by maturation rates (Stringham 1990). Stringham (1984) found a negative correlation with age of sexual maturity and latitude. Our data from an interior southern latitude grizzly bear range indicate little difference in age of first reproduction and sexual maturity when compared to most northern grizzly bear ranges.

The mean reproductive interval of 2.69 in the NCDE was similar to the 2.67 mean interval reported by McLellan (1989). Reproductive interval in grizzly bear is normally 3 or more years (Craighead and Craighead 1969, Smith and Van Daele 1988, and Miller 1990). Confining the reproductive interval in our data to successfully weaned litters and weighting individuals equally raised the mean birth interval for the NCDE nearer the normally reported 3 years.

In the NCDE, 2-year reproductive intervals were recorded frequently. Although uncommon, alternate-year intervals have been reported by other scientists (Craighead et al. 1976, Miller 1990). Some grizzly bears may be demonstrating an increased reproductive rate by producing litters at more frequent intervals. We could not determine if cubs from these accelerated reproductive intervals have a lowered survival.

We observed that some female grizzly bears engaged in breeding activity and conceived while attending yearling offspring. We could not determine the proportion of female grizzly bears that were lactating during breeding season while accompanied by yearlings. Hensel et al. (1969) hypothesized that ovulation was inhibited during lactation. However, he found evidence of follicular activity in 1 female with yearlings. LeCount (1983) reported female black bears ovulating and successfully breeding while lactating. Tsubota et al. (1990) reported ovulation in a female brown bear which was lactating. He suggested that ovulation was not inhibited because the young were already weaned and had eaten wild food. Our field observations indicated that some yearling litters were weaned by breeding season while others were not.

Litter size in the NCDE was similar to those reported for Yellowstone and Canada (Craighead et al. 1976, Knight and Eberhardt 1985, McLellan 1989). Litter size was significantly higher in family groups monitored from den emergence than in those captured and monitored later in summer or fall. Our results demonstrate the importance of radio marking family groups and standardizing the season for comparing litter size. Significant error can result from pooling litters from all seasons after some mortality has occurred.

There is considerable variation in cub and yearling survival and mortality rates reported in the literature (Bunnel and Tait 1985). Percent cub survival in the NCDE appears to be relatively high compared to studies in Alaska or in the Yellowstone Ecosystem prior to 1970 but similar to survival reported in adjacent portions of the NCDE in Canada or the Yellowstone Ecosystem after 1974 (Table 1). Yearling survival was similar to areas in Alaska and Canada with the exception of Kodiak Island and Yellowstone Ecosystem

Table 1. Comparisons of cub and yearling survival rates in North America.

Study area	Source	Cub survival	Yearling survival
Kodiak Island	Smith and Van Daele (1988)	0.625	0.650
South-central Alaska	Miller (1990)	0.660	0.820
North-central Alaska	Reynolds (1990)	0.710	0.930
Yellowstone 1959-67	Craighead et al. (1974)	0.740	0.680
Yellowstone 1974-82	Knight and Eberhardt (1985)	0.890	0.730
Southern B.C.	McLellan (1989)	0.820	0.880
NCDE Montana	This study	0.887	0.863

where yearling survival appears to be relatively low.

The 2 most significant types of mortality experienced by cub and yearling grizzly bears in the NCDE were management control and natural mortality. Natural mortalities observed included suspected male infanticide and an avalanche. Cannibalism or infanticide by male bears is commonly reported in brown bear populations of North America (Troyer and Hensel 1962, Glenn et al. 1976, Smith and Van Daele 1988, Reynolds 1990). In the NCDE we have implicated male bears in the killing of cubs, yearlings, 2-year-olds and at least 1 adult female.

The role of male bears in the population dynamics of bears has been previously contemplated with varying opinions regarding its function in density dependent population regulation (McCullough 1981, Stringham 1983, LeCount 1987). Examples of male bears influencing cub survival rates are reported for Kodiak Island and Yellowstone during the garbage dump era. The high cub mortality in these studies may be a reflection of crowding near concentrated food resources and increased intraspecific strife (Glenn et al. 1976). Cub mortality by male bears could have serious implications in population regulation. Further study to increase sample size and identify causes of cub mortality would be necessary to test a hypothesis that male grizzly bears in the NCDE have a significant impact on cub survival.

Many studies indicate that rates of reproduction and survival in bears are positively correlated with nutritional status of females and food supply (Elowe and Dodge 1990, Stringham 1990). Larger cub litters and higher survival rates may be a function of higher growth rate (Stringham 1990). In the NCDE grizzly bear habitat west of the Continental Divide is perceived as superior, producing relatively abundant bear foods and supporting higher bear densities (Dood et al. 1986, Aune and Kasworm 1989). Results from this study do not conform to a hypothesis that habitat quality explains the difference in reproductive parameters from various portions of the NCDE. We found larger litter sizes and slightly higher survival in a portion of the NCDE generally considered to be poorer quality habitat.

McLellan (1989) observed that density-dependent regulation acts on both reproduction and mortality within the NCDE in Canada. In Montana density-dependent factors could have influenced reproduction and cub survival. We observed larger litters and slightly greater cub survival in the portion of the NDCE with a lower population density. Conversely we saw smaller litters and reduced survival in portions with high population densities. Further study is needed to determine how density dependent factors operate in grizzly bear populations of the NCDE.

Much needs to be learned about the dynamics of grizzly bear populations. Considerable economic costs in marking and sampling populations deters adequate study of grizzly bear cub mortality and survival. The Yellowstone Ecosystem utilizes an ecosystem-wide study design, which successfully monitors female with cub survival and collects survival data for various age classes. In the NCDE opportunities to examine these parameters exist, but require coordinated study efforts and pooling data from the currently fragmented research programs. We recommend that further efforts be made to adequately sample female grizzly bears associated with cubs and pooling data to measure the survival of cubs and yearlings. The scientific collection of these data along with survivorship information from 3- and 4-year-old bears could result in an adequate data base to develop recruitment models. Recruitment modeling would predict the number of cubs necessary to offset losses due to mortality and provide better interpretation of current recovery targets. Current NCDE and Yellowstone Ecosystem population productivity parameters used to monitor population recovery could be enhanced with adequate information regarding population recruitment.

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